The simplest problem in the collective dynamics of neural networks: Is synchrony stable?

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For spiking neural networks we consider the stability problem of global synchrony, arguably the simplest non-trivial collective dynamics in such networks. We find that even this simplest dynamical problem – local stability of synchrony – is non-trivial to solve and requires novel methods for its solution. In particular, the discrete mode of pulsed communication together with the complicated connectivity of neural interaction networks requires a non-standard approach. The dynamics in the vicinity of the synchronous state is determined by a multitude of linear operators, in contrast to a single stability matrix in conventional linear stability theory. This unusual property qualitatively depends on network topology and may be neglected for globally coupled homogeneous networks. For generic networks, however, the number of operators increases exponentially with the size of the network.

We present methods to treat this multi-operator problem exactly. First, based on the Gershgorin and Perron-Frobenius theorems, we derive bounds on the eigenvalues that provide important information about the synchronization process but are not sufficient to establish the asymptotic stability or instability of the synchronous state. We then present a complete analysis of asymptotic stability for topologically strongly connected networks using simple graph-theoretical considerations.

For inhibitory interactions between dissipative (leaky) oscillatory neurons the synchronous state is stable, independent of the parameters and the network connectivity. These results indicate that pulse-like interactions play a profound role in network dynamical systems, and in particular in the dynamics of biological synchronization, unless the coupling is homogeneous and all-to-all. The concepts introduced here are expected to also facilitate the exact analysis of more complicated dynamical network states, for instance the irregular balanced activity in cortical neural networks.

Keywords: Synchronization, networks, graph theory, random matrices, cortical circuits

I. INTRODUCTION

Understanding the collective dynamics of biological neural networks represents one of the most challenging problems in current theoretical biology. For two distinct reasons, the study of synchronization in large neuronal networks plays a paradigmatic role in theoretical studies of neuronal dynamics. Firstly, synchrony is an ubiquitous collective feature of neural activity. Large-scale synchronous activity has been observed by spatially coarse methods such as electro- or magnetoencephalography. Complementing experiments of parallel recordings of spiking activity of individual cells have shown that the synchronization of firing times of indiviual units is often precise with a temporal scatter of the order of a few milliseconds [1, 2]. This precise locking has been observed over significant distances in the cortex and even across hemispheres [3]. Synchronous activity also plays an important role in pathological state such as epileptic seizures [4]. Secondly, the synchronous state is arguably the simplest non-trivial collectively coordinated state of a network dynamical system. Mathematically, it is therefore one of the most throroughly investigated states in the dynamics of biological neural networks. Following the paradigm set by the seminal works of Winfree and Kuramoto on the dynamics of biological oscillators, most studies of synchronization have utilized either temporal or population averaging techniques to map the pulse-coupled dynamics of biological neural networks to effective models of phase-coupled oscillators or density dynamics [5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22].

While this approach has proven to be very informative, it provides exact results only under highly restrictive conditions. In fact, studies approaching the dynamics of biological neural networks using exact methods [7, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34], have over the past decade revealed numerous examples of collective behaviours that obviouslly are outside the standard repertoir of behaviours expected from a smoothly coupled dynamical system. These include several new and unexpected phenomena such as unstable attractors [23, 24, 35], stable chaos [23, 24, 36], topological speed limits to coordinating spike times [31, 32], and extreme sensitivity to network topology [37]. The occurence of these phenomena may signal that the proper theoretical analysis of collective neuronal dynamics mathematically represents a much more challenging task than is currently appreciated.

In this article, we study the impact of pulse-coupling, delayed interactions and complicated network connectivity on the exact microscopic dynamics of neural networks and expose the mathematical complexity that emerges already when considering the seemingly simple problem of neuronal synchronization. Utilizing the Mirollo-Strogatz phase representation of individual units, we present an analytical treatment of finite networks of arbitrary connectivity.

The results obtained unearth an unanticipated subtlety of the nature of this stability problem: It turns out that a single linear operator is not sufficient to represent the local dynamics in these systems. Instead, a large number of linear operators, depending on rank order of the perturbation vector, is needed to represent the dynamics of small perturbations. We present methods to characterize the eigenvalues of all operators arising for a given network. Universal properties of the stability operators lead to exact bounds on the eigenvalues of all operators and also provide a simple way to prove plain but not asymptotic stability for any network. We then show for topologically strongly connected networks that asymptotic stability of the synchronized state can be demonstrated by graph-theoretical considerations. We find that for inhibitory interactions the synchronous state is stable, independent of the parameters and the network connectivity. A part of this work that considers plain (non-asymptotic) stability without networks constraints has been briefly reported before for the case of inhibitory coupling [38].These results indicate that pulse-like interactions play a profound role in network dynamical systems, and in particular in the dynamics of biological synchronization, unless the coupling is homogeneous and all-to-all. They highlight the need for exact mathematical tools that can handle the dynamic complexity of neuronal systems at the microscopic level.

II. THE PHASE REPRESENTATION OF PULSE-COUPLED NETWORKS

We consider networks of N pulse-coupled oscillatory units, neurons, with delayed interactions. A phase-like variable $\phi_j(t) \in (-\infty, 1]$ specifies the state of each oscillator j at time t such that the difference between the phases of two oscillators quantifies their degree of synchrony, with identical phases for completely synchronous oscillators. The free dynamics of oscillator j is given by

$$\frac{d\phi_j}{dt} = 1. \tag{1}$$

Whenever oscillator j reaches a threshold

$$\phi_j(t) = 1 \tag{2}$$

the phase is reset to zero

$$\phi_j(t^+) = 0 \tag{3}$$

and a pulse is sent to all other post-synaptic oscillators $i \in \text{Post}(j)$. These oscillators i receive this signal after a delay time τ. The interactions are mediated by a function $U(\phi)$ specifying a 'potential' of an oscillator at phase ϕ. The function U is assumed twice continuously differentiable, monotonically increasing,

$$U' > 0, \tag{4}$$

concave (down),

$$U'' < 0, \tag{5}$$

and normalized such that

$$U(0) = 0 \quad \text{and} \quad U(1) = 1. \tag{6}$$

For a general $U(\phi)$ we define the transfer function

$$H_\varepsilon(\phi) = U^{-1}(U(\phi) + \varepsilon) \tag{7}$$

that represents the response of an oscillator at phase ϕ to an incoming sub-threshold pulse of strength ε. Depending on whether the input ε_{ij} received by oscillator i from j is sub-threshold,

$$U(\phi) + \varepsilon_{ij} < 1, \tag{8}$$

or supra-threshold,

$$U(\phi) + \varepsilon_{ij} \geq 1, \tag{9}$$

the pulse sent at time t (Eq. (2)) induces a phase jump after a delay time τ at time $t + \tau$ according to

$$\phi_i((t+\tau)^+) = \begin{cases} H_{\varepsilon_{ij}}(\phi_i(t+\tau)) & \text{if } U(\phi_i(t+\tau)) + \varepsilon_{ij} < 1 \\ 0 & \text{if } U(\phi_i(t+\tau)) + \varepsilon_{ij} \geq 1 \end{cases}. \tag{10}$$
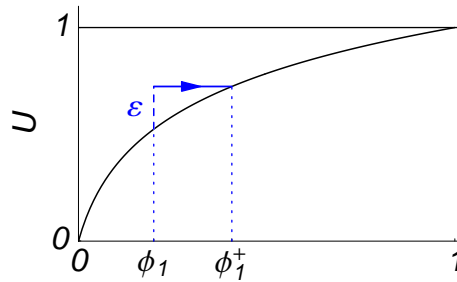
Figure 1: An incoming pulse of strength ε induces a phase jump $\phi_1^+ := \phi_1(t^+) = U^{-1}(U(\phi_1(t)) + \varepsilon) = H_\varepsilon(\phi_1)$ that depends on the state $\phi_1 := \phi_1(t)$ of the oscillator at time t of pulse reception. Due to the curvature of U, an excitatory pulse ($\varepsilon > 0$) induces an advancing phase jump. If the incoming pulse puts the potential above threshold ($U(\phi_1) + \varepsilon > 1$), the phase is reset to zero ($\phi_1^+ = 0$). An inhibitory pulse ($\varepsilon < 0$) would induce a regressing phase jump such that the phase may assume negative values (not shown).

In the second case also a pulse is emitted by oscillator i . The phase jump (Fig. 1) depends on the phase $\phi_i(t+\tau)$ of the receiving oscillator i at time $t+\tau$ after the signal by oscillator j has been sent at time t, the effective coupling strength ε_{ij}, and the nonlinear potential function U. The interaction from unit j to unit i is either excitatory ($\varepsilon_{ij} > 0$) inducing advancing phase jumps (cf. Fig. 1) or inhibitory ($\varepsilon_{ij} < 0$) inducing retarding phase jumps. If there is no interaction from j to i, we have $\varepsilon_{ij} = 0$ and . There are two immediate differences between inhibitory and excitatory inputs. First, while inhibitory input $\varepsilon_{ij} < 0$ is always sub-threshold, excitatory input $\varepsilon_{ij} > 0$ may also be supra-threshold and thus induce an instantaneous reset to zero according to Eq. (10). Second, in response to the reception of an inhibitory pulse, the phases of the oscillators may assume negative values whereas for excitatory coupling they are confined to the interval $[0, 1]$. We remark here that we do not consider the dynamics (and perturbations) of variables that encode the spikes in transit, i.e. spikes that have been sent but not yet received at any instant of time. These additional variables make the system formally higher-dimensional. However, under the conditions considered below, in particular for networks of identical neurons with inhibitory interactions, earlier rigorous work [35] shows that these spike time variables lock to the phase variables once all spikes present in the system initially have arrived and every neuron has emitted at least one spike thereafter (which takes finite total time). Thus, for our purposes, we consider the dynamics and perturbations of the phase variables only.

Choosing appropriate functions U the dynamics of a wide variety of pulse coupled systems can be represented. In particular, any differential equation for an individual neural oscillator of the form

$$\dot{V}_i = f(V_i) + S_i(t) \tag{11}$$

together with the threshold firing condition

$$V_i(t) = 1 \Rightarrow V_i(t^+) = 0 \tag{12}$$

where

$$S_i(t) = \sum_{j,m} \varepsilon_{ij}\delta(t - t_{j.m}) \tag{13}$$

is the synaptic current from the network and $t_{j,m}$ is the time of the mth firing of neuron j. As long as the free ($S_i(t) \equiv 0$) dynamics has a periodic solution $V(t)$ with period T and negative curvature, the function U can be taken as the scaled solution,

$$U(\phi) := V(\phi T). \tag{14}$$

Thus a general class of pulse-coupled oscillator networks, defined by Eq. (11-13), can be mapped onto the normalized phase representation (Eqs. (1)–(10)).

In this paper, we consider a system of N coupled Mirollo-Strogatz oscillators which interact on directed graphs by sending and receiving pulses. The structure of this graph is specified by the sets $\mathrm{Pre}(i)$ of presynaptic oscillators that send pulses to oscillator i. For simplicity we assume no self-interactions, $i \notin \mathrm{Pre}(i)$. The sets $\mathrm{Pre}(i)$ completely determine the topology of the network, including the sets $\mathrm{Post}(i)$ of postsynaptic oscillators that receive pulses from i. The coupling strength between oscillator j and oscillator i is given by ε_{ij} such that

$$\begin{aligned} \varepsilon_{ij} \neq 0 \quad &\text{if } j \in \mathrm{Pre}(i) \\ \varepsilon_{ij} = 0 \quad &\text{otherwise.} \end{aligned} \tag{15}$$

Thus a connection is considered to be present if the connection strength is non-zero. All analytical results presented are derived for the general class of interaction functions U introduced above. The structure of the network is completely arbitrary except for the restriction that every oscillator has at least one presynaptic oscillator.

III. REGULAR AND IRREGULAR DYNAMICS IN PULSE-COUPLED NETWORKS

The synchronous state in which

$$\phi_i(t) = \phi_0(t) \quad \text{for all } i \tag{16}$$

is arguably one of the simplest ordered states a network of pulse-coupled oscillators may assume. This synchronous state exists if and only if the coupling strengths are normalized such that

$$\sum_{j \in \mathrm{Pre}(i)} \varepsilon_{ij} = \varepsilon. \tag{17}$$

One should keep in mind that this state whether stable or not is typically not a global attractor in complex networks. To illustrate this point let us briefly consider a specific example. Figures (Fig. 2 and 3) show numerical results from a in a randomly connected network of integrate-and-fire oscillators where $U(\phi) = U_{\mathrm{IF}}(\phi) = I(1 - e^{-\phi T_{\mathrm{IF}}})$ and $T_{\mathrm{IF}} = \ln(I/(I-1))$ with strong interactions. This network exhibits a balanced state (cf. [16, 39, 40]) characterized by irregular dynamics. In this balanced state, found originally in binary neural networks [39, 40], inhibitory and excitatory inputs cancel each other on average but fluctuations lead to a variability of the membrane potential and a high irregularity in firing times (see also [16]). Figures 2a,b display sample trajectories of the potentials $U(\phi_i)$ of three oscillators for the same random network, making obvious the two distinct kinds of coexisting dynamics. Whereas in the synchronous state all oscillators display identical periodic dynamics, in the balanced state oscillators fire irregularly, asynchronous, and in addition differ in their firing rates.
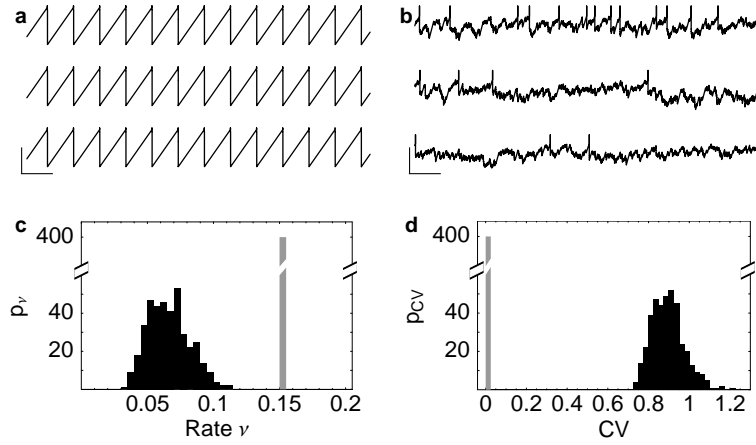

Figure 2: Coexistence of (a) synchronous and (b) irregular dynamics in a random network ($N = 400$, $p = 0.2$, $I = 4.0$, $\varepsilon = -16.0$, $\tau = 0.035$), cf. [38]. (a),(b): Trajectories of the potential $U(\phi_i)$ of three oscillators (angular bars: time scale (horizontal) $\Delta t = 8$; potential scales (vertical) (a) $\Delta U = 8$, (b) $\Delta U = 2$; spikes of height $\Delta U = 1$ added at firing times). (c),(d): Distributions (c) p_ν of rates and (d) p_{CV} of the coefficient of variation, displayed for the irregular (dark gray) and synchronous (light gray) dynamics. Figure modified from [38].

The latter dynamical difference is quantified by a histogram p_ν of oscillator rates (Fig. 2c)

$$\nu_i = \left(\langle t_{i,n+1} - t_{i,n} \rangle_n \right)^{-1}, \tag{18}$$

the reciprocal values of the time averaged inter-spike intervals. Here the $t_{i,n}$ are the times when oscillator i fires the nth time. The temporal irregularity of the firing-sequence of single oscillators i is measured by the coefficient of variation

$$CV_i = \left(\nu_i^2 \left\langle (t_{i,n+1} - t_{i,n})^2 \right\rangle_n - 1 \right)^{\frac{1}{2}}, \tag{19}$$

defined as the ratio of the standard deviation of the inter-spike intervals and their average. A histogram p_{CV} of the CV_i shows that the irregular state exhibits coefficients of variation near one, the coefficient of variation of a Poisson process. Such irregular states occur robustly when changing parameters and network topology.

Figure 3 illustrates the bistability of these qualitatively different states by switching the network dynamics form one state to the other by external perturbations. A simple mechanism to synchronize oscillators that are in a state of irregular firing is the delivery of two sufficiently strong external excitatory (phase-advancing) *pulses* that are separated by a time $\Delta t \in (\tau, 1)$, cf. Fig. 3. The first pulse then leads to a synchronization of phases due to simultaneous supra-threshold input, cf. (7). If there are traveling signals that have been sent but not received at the time of the first pulse, a second pulse after a time $\Delta t > \tau$ is needed that synchronizes the phases after all internal signals have been received. In this network the synchronous state is not affected by *small random perturbations*, whereas *large random perturbations* lead back to irregular dynamics (Fig. 3). These features clearly suggests that the synchronized states is an asymptotically stable local attractor. However, with the exception of special cases no exact treatment of this proposition exists. Below we will expose that a general treatment of the stability of apparently simple synchronous state reveals an unexpectedly complex mathematical setting.
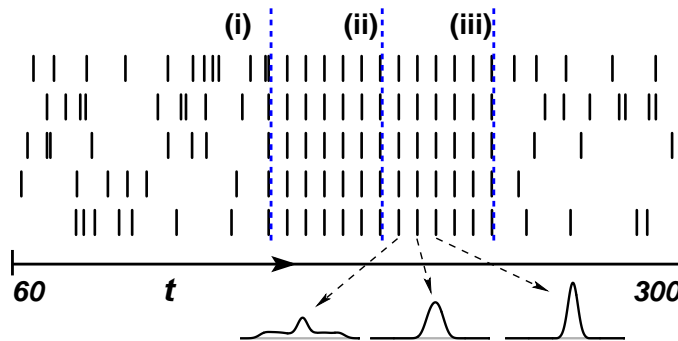

Figure 3: Switching between irregular and synchronous dynamics ($N = 400$, $p = 0.2$, $I = 4.0$, $\varepsilon = -16.0$, $\tau = 0.14$). Firing times of five oscillators are shown in a time window $\Delta t = 240$. Vertical dashed lines mark external perturbations: (i) large excitatory pulses lead to synchronous state, (ii) a small random perturbation ($|\Delta \phi_i| \leq 0.18$) is restored, (iii) a sufficiently large random perturbation ($|\Delta \phi_i| \leq 0.36$) leads to an irregular state. Bottom: Time evolution of the spread of the spike times after perturbation (ii), total length $\Delta t = 0.25$ each. Figure modified from [38].

IV.   CONSTRUCTING STROBOSCOPIC MAPS

We perform a stability analysis of the synchronous state

$$\phi_i(t) = \phi_0(t) \quad \text{for all } i \tag{20}$$

in which all oscillators display identical phase-dynamics $\phi_0(t)$ on a periodic orbit such that $\phi_0(t + T) = \phi_0(t)$. The period of the synchronous state is given by

$$T = \tau + 1 - \alpha \tag{21}$$

where

$$\alpha = U^{-1}(U(\tau) + \varepsilon). \tag{22}$$

For simplicity, we consider the cases where the total input ε is sub-threshold, $U(\tau) + \varepsilon < 1$ such that $\alpha < 1$. A perturbation

$$\boldsymbol{\delta}(0) =: \boldsymbol{\delta} = (\delta_1, \ldots, \delta_N) \tag{23}$$

to the phases is defined by

$$\delta_i = \phi_i(0) - \phi_0(0). \tag{24}$$

If we assume that the perturbation is small in the sense that

$$\max_i \delta_i - \min_i \delta_i < \tau \tag{25}$$

this perturbation can be considered to affect the phases of the oscillators at some time just after all signals have been received, i.e. after a time $t > t_0 + \tau$ if all oscillators have fired at $t = t_0$. This implies that in every cycle, first each neuron sends a spike before any neuron receives any spike. Such a perturbation will affect the time of the next firing events because the larger the perturbed phase of an oscillator is, the earlier this oscillator reaches threshold and sends a pulse. In principle, there one may consider other perturbations, in which, for instance, a pulse is added or removed at a certain time. As such perturbations are not relevant for questions of asymptotic stability, we do not consider them here.

To construct the stroboscopic period-T map, it is convenient to rank order the elements δ_i of $\boldsymbol{\delta}$ in the following manner: For each oscillator i we label the perturbations δ_j of its presynaptic oscillators $j \in \mathrm{Pre}(i)$ (for which $\varepsilon_{ij} \neq 0$) according to their sizes

$$\Delta_{i,1} \geq \Delta_{i,2} \geq \ldots \geq \Delta_{i,k_i} \tag{26}$$

where

$$k_i := |\mathrm{Pre}(i)| \tag{27}$$

is the number of its presynaptic oscillators, called in-degree in graph theory. The index $n \in \{1, \ldots, k_i\}$ counts the received pulses in the order of their successive arrival. Thus, if $j_n \equiv j_n(i) \in \mathrm{Pre}(i)$ labels the presynaptic oscillator from which i receives its nth signal during the period considered, we have

$$\Delta_{i,n} = \delta_{j_n(i)} . \tag{28}$$

For later convenience, we also define

$$\Delta_{i,0} = \delta_i . \tag{29}$$

For illustration, let us consider an oscillator i that has exactly two presynaptic oscillators j and j' such that $\mathrm{Pre}(i) = \{j, j'\}$ and $k_i = 2$ (Fig. 4a,d). For certain perturbations, oscillator i first receives a pulse from oscillator j'
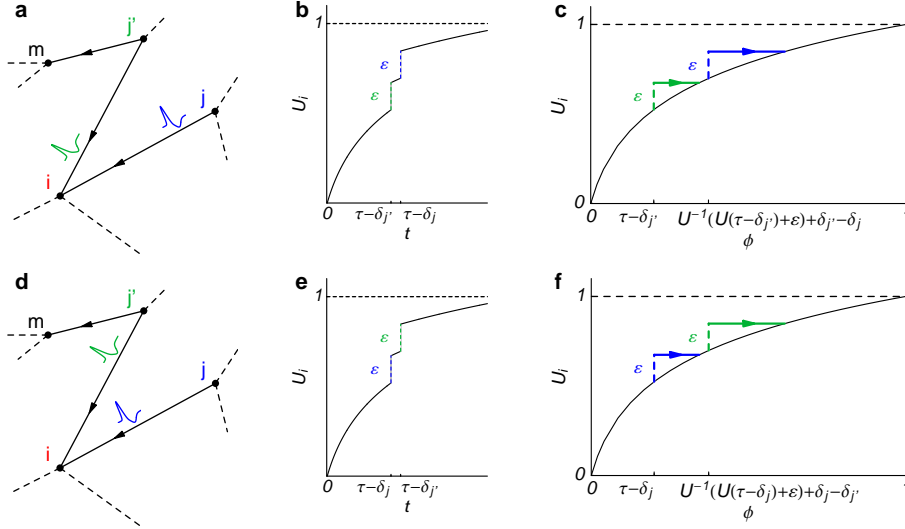

Figure 4: Two signals arriving almost simultaneously induce different phase changes, depending on their rank order. The figure illustrates a simple case where $\mathrm{Pre}(i) = \{j, j'\}$ and $\delta_i = 0$, (a)–(c) for $\delta_{j'} > \delta_j$ and (d)–(f) for $\delta_j > \delta_{j'}$. (a), (d) Local patch of the network displaying the reception times of signals that are received by oscillator i. Whereas in (a) the signal from j' arrives before the signal of j, the situation in (d) is reversed. (b), (e) Identical coupling strengths induce identical jumps of the *potential* U but (c),(f) the *phase* jumps these signals induce are different and depend on the order of the incoming signals. For small $|\delta_i| \ll 1$, individual phase jumps are encoded by the $p_{i,n}$.

and later from oscillator j. This determines the rank order, $\delta_{j'} > \delta_j$, and hence $\Delta_{i,1} = \delta_{j'}$ and $\Delta_{i,2} = \delta_j$ (Fig. 4a). Perturbations with the opposite rank order, $\delta_j > \delta_{j'}$, lead to the opposite labeling, $\Delta_{i,1} = \delta_j$ and $\Delta_{i,2} = \delta_{j'}$ (Fig. 4d).

We now consider a fixed, arbitrary, perturbation, the rank order of which determines the $\Delta_{i,n}$ according to the inequalities (26). Using the phase shift function $H_\varepsilon(\phi)$ (see (7)) and denoting

$$D_{i,n} := \Delta_{i,n-1} - \Delta_{i,n} \tag{30}$$

for $n \in \{1, \ldots, k_i\}$ we calculate the time evolution of phase-perturbations δ_i satisfying (25). Without loss of generality, we choose an initial condition near $\phi_0(0) = \tau/2$. The stroboscopic time-T map of the perturbations, $\delta_i \mapsto \delta_i(T)$, is obtained from the scheme given in Table I. The time to threshold of oscillator i, which is given in the lower left of

t	$\phi_i(t)$
0	$\frac{\tau}{2} + \delta_i =: \frac{\tau}{2} + \Delta_{i,0}$
$\frac{\tau}{2} - \Delta_{i,1}$	$U^{-1}(U(\tau + D_{i,1}) + \varepsilon_{ij_1}) =: \beta_{i,1}$
$\frac{\tau}{2} - \Delta_{i,2}$	$U^{-1}(U(\beta_{i,1} + D_{i,2}) + \varepsilon_{ij_2}) =: \beta_{i,2}$
$\vdots$	$\vdots$
$\frac{\tau}{2} - \Delta_{i,k_i}$	$U^{-1}(U(\beta_{i,k_i-1} + D_{i,k_i}) + \varepsilon_{ij_{k_i}}) =: \beta_{i,k_i}$
$\frac{\tau}{2} - \Delta_{i,k_i} + 1 - \beta_{i,k_i}$	reset: $1 \mapsto 0$

Table I: Time evolution of oscillator i in response to k_i successively incoming signals from its presynaptic oscillators j_n, $n \in \{1, \ldots, k_i\}$, from which i receives the nth signal during this period. The right column gives the phases $\phi_i(t)$ at times t given in the left column. The time evolution is shown for a part of one period ranging from $\phi_i \approx \tau/2$ to reset, $1 \to 0$, such that $\phi_i = 0$ in the last row. The first row gives the initial condition $\phi_i(0) = \tau/2 + \delta_i$. The following rows describe the reception of the k_i signals during this period whereby the phases are mapped to $\beta_{i,n}$ after the nth signal has been received. The last row describes the reset at threshold such that the respective time $T_i^{(0)} = \tau/2 - \Delta_{i,k_i} + 1 - \beta_{i,k_i}$ gives the time to threshold of oscillator i.

the scheme,

$$T_i^{(0)} := \frac{\tau}{2} - \Delta_{i,k_i} + 1 - \beta_{i,k_i} \tag{31}$$

is about $\phi_0(0) = \tau/2$ smaller than the period T. Hence the period-T map of the perturbation can be expressed as

$$\delta_i(T) = T - T_i^{(0)} - \frac{\tau}{2} = \beta_{i,k_i} - \alpha + \Delta_{i,k_i} \tag{32}$$

where α is given by Equation (22).

Equation (32) defines a map valid for one particular rank order of perturbations. In general, the perturbations of all k_i presynaptic oscillators of oscillator i lead to $k_i!$ different possibilities of ordering. Thus the number of possible maps, μ, is bounded by

$$\left(\max_i k_i\right)! \leq \mu \leq (N-1)! \,. \tag{33}$$

Here the minimum is assumed, $\mu = (\max_i k_i)!$, if only one oscillator has exactly μ presynaptic oscillators and all other oscillators have exactly one presynaptic oscillator. The maximum, $\mu = (N-1)!$, is assumed if the oscillators are coupled all-to-all such that all connections are present, $\varepsilon_{ij} \neq 0$ for all i and $j \neq i$. If the coupling is all-to-all and in addition homogeneous, $\varepsilon_{ij} = \varepsilon/(N-1)$ for all i and $j \neq i$, all maps are equivalent in the sense that for any pair of maps there is a permutation of oscillator indices that transforms one map onto the other. For general network connectivities, however, there is no such permutation equivalence. For instance, in random networks with N vertices and edges that are independently chosen with identical probability p, the number of maps increases strongly with N.

V. MULTI-OPERATOR DYNAMICS OF SMALL PERTURBATIONS

In order to perform a local stability analysis, we consider the first order approximations of the maps derived in the previous section. Expanding β_{i,k_i} for small $D_{i,n} \ll 1$ one can proof by induction (see Appendix) that to first order

$$\beta_{i,k_i} \doteq \alpha + \sum_{n=1}^{k_i} p_{i,n-1} D_{i,n} \tag{34}$$

where

$$p_{i,n} := \frac{U'(U^{-1}(U(\tau) + \sum_{m=1}^{n} \varepsilon_{ij_m}))}{U'(U^{-1}(U(\tau) + \varepsilon))} \tag{35}$$

for $n \in \{0, 1, \ldots, k_i\}$ encodes the effect of an individual incoming signal of strength ε_{ij_n}. The statement $x \doteq y$ means that $x = y + \sum_{i,n} \mathcal{O}(D_{i,n}^2)$ as all $D_{i,n} \to 0$. Substituting the first order approximation (34) into (32) using (30) leads to

$$\delta_i(T) \doteq \sum_{n=1}^{k_i} p_{i,n-1}(\Delta_{i,n-1} - \Delta_{i,n}) + \Delta_{i,k_i} \tag{36}$$

such that after rewriting

$$\delta_i(T) \doteq p_{i,0}\Delta_{i,0} + \sum_{n=1}^{k_i} (p_{i,n} - p_{i,n-1})\Delta_{i,n} \tag{37}$$

to first order in all $\Delta_{i,n}$. Since $\Delta_{i,n} = \delta_{j_n(i)}$ for $n \in \{1, \ldots, k_i\}$ and $\Delta_{i,0} = \delta_i$ according to Eqs. (28) and (29), this represents a linear map

$$\boldsymbol{\delta}(T) \doteq A\boldsymbol{\delta} \tag{38}$$

where the elements of the matrix A are given by

$$A_{ij} = \begin{cases} p_{i,n} - p_{i,n-1} & \text{if } j = j_n \in \text{Pre}(i) \\ p_{i,0} & \text{if } j = i \\ 0 & \text{if } j \notin \text{Pre}(i) \cup \{i\}. \end{cases} \tag{39}$$

Because j_n in (39) identifies the nth pulse received during this period by oscillator i, the first order operator depends on the rank order of the perturbations, $A = A(\text{rank}(\boldsymbol{\delta}))$. The map $A\boldsymbol{\delta}$ consists of a number of linear operators, the domains of which depend on the rank order of the specific perturbation. Thus $A\boldsymbol{\delta}$ is piecewise linear in $\boldsymbol{\delta}$. This map is continuous but not in general differentiable at the domain boundaries where $\delta_i = \delta_j$ for at least one pair i and j of oscillators. In general, signals received at similar times by the same oscillator induce different phase changes: For the above example of an oscillator i with exactly two presynaptic oscillators j and j' and equal coupling strengths, $\varepsilon_{i,j} = \varepsilon_{i,j'}$, the first of the two received signals has a larger effect than the second, by virtue of the concavity of $U(\phi)$. For small $|\delta_i| \ll 1$, this effect is encoded by the $p_{i,n}$ (see Eq. (35) and the Appendix for details). Since the matrix elements Eq. (39) are differences of these $p_{i,n}$ the respective matrix elements $A_{i,j}$ and $A_{i,j'}$ have in general different values depending on which signal is received first. This is induced by the structure of the network in conjunction with the pulse coupling. For networks with homogeneous, global coupling different matrices A can be identified by an appropriate permutation of the oscillator indices. In general, however, this is impossible.

VI. BOUNDS ON THE EIGENVALUES

The above consideration establish that for many network structures when considering the stability of the synchronous state one is faced with the task of characterizing a large number of operators instead of a single stability matrix. Fortunately it is possible to characterize spectral properties common to all operators by studying bounds on their eigenvalues.

A. General properties of matrix elements

It is important to observe that the matrix elements defined by Eqs. (38) and (39) are normalized row-wise,

$$\sum_{j=1}^{N} A_{ij} = A_{ii} + \sum_{\substack{j=1 \\ j \neq i}}^{N} A_{ij} \tag{40}$$

$$= A_{ii} + \sum_{n=1}^{k_i} A_{ij_n} \tag{41}$$

$$= p_{i,0} + \sum_{n=1}^{k_i} (p_{i,n} - p_{i,n-1}) \tag{42}$$

$$= p_{i,k_i} \tag{43}$$

$$= 1 \tag{44}$$

for all i. Here the second last equality holds because the telescope sum equals $p_{i,k_i} - p_{i,0}$. Therefore, every matrix A has the trivial eigenvalue

$$\lambda_1 = 1 \tag{45}$$

corresponding to the eigenvector

$$v_1 = (1, 1, \ldots, 1)^\mathsf{T} \tag{46}$$

reflecting the time-translation invariance of the system. In addition, the diagonal elements

$$A_{ii} = p_{i,0} = \frac{U'(\tau)}{U'(U^{-1}(U(\tau) + \varepsilon))} =: A_0 \tag{47}$$

are identical for all i. Since U is monotonically increasing, $U'(\phi) > 0$ for all ϕ, the diagonal elements are positive,

$$A_0 > 0. \tag{48}$$

One should note that the matrices A have the properties (40)–(48) independent of single neuron parameters, the network connectivity, and the specific perturbation considered. Due to the above properties of the stability matrices, bounds on the eigenvalues of a specific matrix A can be obtained from the Gershgorin theorem [41] (see also [42]).

Theorem VI.1 (Gershgorin) *Given an $N \times N$ matrix $A = (A_{ij})$ and disks*

$$K_i := \{z \in \mathbb{C} | \ |z - A_{ii}| \leq \sum_{\substack{j=1 \\ j \neq i}}^{N} |A_{ij}|\} \tag{49}$$

for $i \in \{1, \ldots, N\}$. Then the union

$$K := \bigcup_{i=1}^{N} K_i \tag{50}$$

contains all eigenvalues of A.

Let us remark that for real matrices A the disks K_i in the complex plane are centered on the real axis at $A_{ii} = A_0$.

B. Eigenvalues for inhibitory coupling

As an application of this theorem to the above eigenvalue problem, we consider the class of networks of inhibitorily coupled oscillators, where all $\varepsilon_{ij} \leq 0$ and $\varepsilon < 0$. In these cases, all nonzero matrix elements A_{ij} are positive: Since $U(\phi)$ is monotonically increasing, $U' > 0$, and concave (down), $U'' < 0$, its derivative U' is positive and monotonically decreasing. Thus all $p_{i,n}$ (Eq. (35)) are positive, bounded above by one,

$$0 < p_{i,n} \leq 1, \tag{51}$$

and increase with n,

$$p_{i,n-1} < p_{i,n}. \tag{52}$$

Hence the nonzero off-diagonal elements are positive, $A_{ij_n} = p_{i,n} - p_{i,n-1} > 0$ such that

$$A_{ij} \geq 0 \tag{53}$$

for all $i, j \in \{1, \ldots, N\}$ and

$$0 < A_0 < 1. \tag{54}$$

As a consequence, for inhibitorily coupled oscillators,

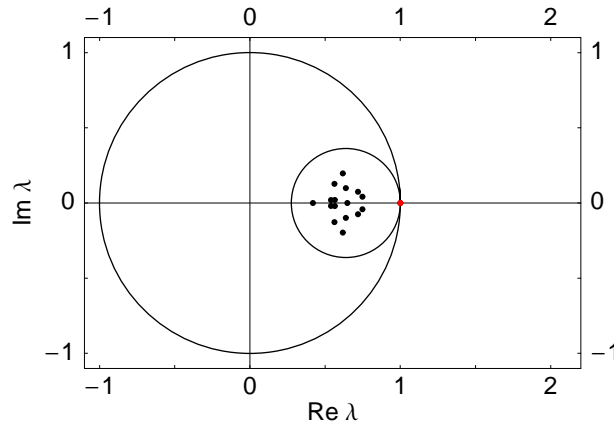$$\sum_{\substack{j=1 \\ j \neq i}}^{N} |A_{ij}| = \sum_{j=1}^{N} A_{ij} - A_{ii} = 1 - A_0 \tag{55}$$

Figure 5: Eigenvalues in the complex plane for inhibitory coupling. The Gershgorin disk, that contacts the unit disk from the inside, contains all eigenvalues of the stability matrices A. Black dots show eigenvalues of a specific stability matrix for a network of $N = 16$ oscillators (in which every connection is present with probability $p = 0.25$) with coupling strengths $\varepsilon_{ij} = \varepsilon/k_i$, $\varepsilon = -0.2$, $\tau = 0.15$, and a particular rank order of the perturbation.

such that all Gershgorin disks K_i are identical and the disk

$$K_i = K = \{z \in \mathbb{C}|\ |z - A_0| \leq 1 - A_0\} \tag{56}$$

contains all eigenvalues of A. This disk K contacts the unit disk from the inside at the trivial eigenvalue $z = \lambda_1 = 1$ (Fig. 5).

Since the unit circle separates stable from unstable eigenvalues and structural perturbations may move any but the trivial unit eigenvalue, it is interesting to examine whether the unite eigenvalues may be degenerate. For strongly connected networks the Perron-Frobenius theorem implies that this eigenvalue is unique demonstrating the structural stability of the confinement of eigenvalues to the unit circle.

If the network is strongly connected, the resulting stability matrix A is irreducible such that the Perron-Frobenius theorem [43, 44, 45, 46] (see also [47, 48]) is applicable (we only state the theorem partially).

Theorem VI.2 (Perron-Frobenius) *Let A be an $N \times N$ irreducible matrix with all its elements real and non-negative. Then*

- *A has a real positive eigenvalue λ_{max}, the maximal eigenvalue, which is simple and such that all eigenvalues λ_i of A satisfy $|\lambda_i| \leq \lambda_{max}$.*

The Perron-Frobenius theorem implies, that the eigenvalue that is largest in absolute value, here $\lambda_1 = 1$, is unique for strongly connected networks. The Gershgorin theorem guarantees that eigenvalues λ of modulus one are degenerate, $\lambda = \lambda_1 = 1$. Taken together, for strongly connected networks, the non-trivial eigenvalues λ_i satisfy

$$|\lambda_i| < 1 \tag{57}$$

for $i \in \{2, \dots, N\}$. This suggests that the synchronous state is stable for inhibitory couplings. As pointed out below (Sec. VII a proof of stability, however, requires further analysis.

C. Eigenvalues for excitatory coupling

Let us briefly discuss the case of excitatorily coupled oscillators, where all $\varepsilon_{ij} \geq 0$ and $\varepsilon > 0$. Here the analysis proceeds similar to the case of inhibitory coupling. Due to the monotonicity and concavity of $U(\phi)$, we obtain

$$p_{i,n} \geq 1 \tag{58}$$

as well as a decrease with n,

$$p_{i,n-1} > p_{i,n}\,, \tag{59}$$

such that $A_{i,j_n} = p_{i,n} - p_{i,n-1} < 0$ and thus

$$A_{ij} \leq 0 \tag{60}$$

for $i \in \{1, \ldots, N\}$ and $j \neq i$ and

$$A_{ii} = A_0 > 1. \tag{61}$$

Consequently, for excitatorily coupled oscillators,

$$\sum_{\substack{j=1 \\ j \neq i}}^{N} |A_{ij}| = -\sum_{\substack{j=1 \\ j \neq i}}^{N} A_{ij} = A_0 - 1 \tag{62}$$

such that again all Gershgorin disks K_i are identical and

$$K_i = K = \{z \in \mathbb{C}| \ |z - A_0| \leq A_0 - 1\}. \tag{63}$$

Since $A_0 > 1$, the disk K contacts the unit disk from the outside at $z = \lambda_1 = 1$ (Fig. 6). If the network is strongly
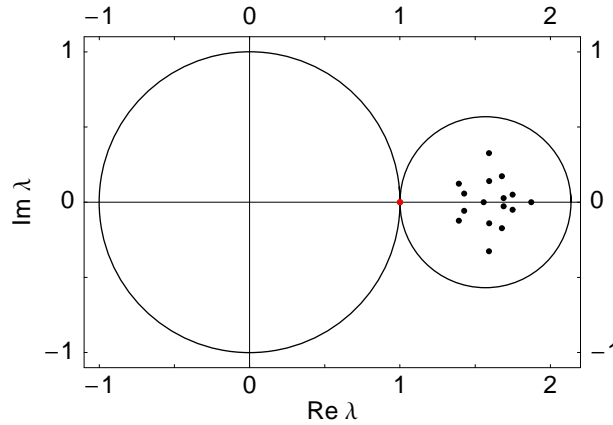

Figure 6: Eigenvalues in the complex plane for excitatory coupling. Gershgorin disk, that contacts the unit disk from the outside, contains all eigenvalues of the stability matrices A. Black dots show eigenvalues of a specific stability matrix for a network of $N = 16$ oscillators (in which every connection is present with probability $p = 0.25$) with coupling strength $\varepsilon_{ij} = \varepsilon/k_i$, $\varepsilon = 0.2$, $\tau = 0.15$) and a particular rank order of the perturbation.

connected, $\lambda_1 = 1$ is again unique by the Perron-Frobenius theorem for irreducible matrices because it is the largest eigenvalue (in absolute value) of the inverse A^{-1} of A, if the inverse exists. This result indicates that the fully synchronous state is unstable for excitatory couplings.

VII. STABILITY

In Sec. VI, we found analytical bounds on the eigenvalues of the stability matrices. However, even if only eigenvalues λ with $|\lambda| \leq 1$ are present, a growth of perturbations might seem to be possible because (i) the eigenspaces of the (asymmetric) matrices A cannot be guaranteed to be orthogonal, and (ii) in general, different matrices A are successively applied to a given perturbation. Due to the non-orthogonality (i) the length $\|\boldsymbol{\delta}\|$ of a given perturbation vector $\boldsymbol{\delta}$ might increase during one period. Since the stability matrix and the set of eigenvectors may change due to (ii), the length of the perturbation vector might increase in the subsequent period as well. Since this procedure may be iterated, the eigenvalues λ_i of the stability matrices, although satisfying $|\lambda_i| < 1$ for $i \in \{2, \ldots, N\}$ and $\lambda_1 = 1$, are not sufficient to ensure the stability of the synchronous state.

Thus, the eigenvalues of the dynamically changing stability matrices guide the intuition about the stability of the synchronous state as well as about the speed of convergence (in case of stability) or divergence (in case of instability). Nevertheless, stability cannot be directly inferred from the set of eigenvalues. In the following we illustrate the final proof of stability in the simple case of inhibitory coupling where all $A_{ij} \geq 0$ (53).

A. Plain stability for inhibitory coupling

For inhibitory networks, the proof of plain (non-asymptotic) stability is simple. Given the fact that for inhibition $\sum_{j=1}^{N} A_{ij} = 1$ and $A_{ij} \geq 0$, the synchronous state is stable because a given perturbation $\boldsymbol{\delta} = \boldsymbol{\delta}(0)$ satisfies

$$\|\boldsymbol{\delta}(T)\| \; := \; \max_i |\delta_i(T)| \tag{64}$$

$$= \; \max_i \left| \sum_{j=1}^{N} A_{ij} \delta_j \right| \tag{65}$$

$$\leq \; \max_i \sum_j |A_{ij}||\delta_j| \tag{66}$$

$$\leq \; \max_i \sum_j |A_{ij}| \max_k |\delta_k| \tag{67}$$

$$= \; \max_i \sum_j A_{ij} \max_k |\delta_k| \tag{68}$$

$$= \; \max_k |\delta_k| \tag{69}$$

$$= \; \|\boldsymbol{\delta}\| \; . \tag{70}$$

In this section, we use the vector norm

$$\|\boldsymbol{\delta}\| := \max_i \delta_i \; . \tag{71}$$

Thus the length of a perturbation vector can not increase during one period implying that it does not increase asymptotically. This result is independent of the connectivity structure of the network, the special choice of parameters, $\varepsilon_{ij} \leq 0$, $\tau > 0$, the potential function $U(\phi)$, and the rank order of the perturbation.

B. Asymptotic stability in strongly connected networks

Asymptotic stability can be established for networks of inhibitorily coupled oscillators assuming that the network satisfies the condition of strong connectivity. A directed graph is called strongly connected if that every vertex can be reached from every other vertex by following the directed connections. Thus a network is strongly connected, if every oscillator can communicate with each oscillator in the network at least indirectly. It is clear that in a disconnected network only the connected components may synchronize completely in the long-term, but these components can not be synchronized by mutual interactions. In the proof given below, we do not consider networks that are disconnected. We do also not consider networks that are weakly connected (but not strongly connected) such as two globally coupled sub-networks which are linked by unidirectional connections from one sub-network to the other.

The synchronous state may be characterized by a perturbation $\boldsymbol{\delta} \equiv \boldsymbol{\delta}(0)$ that represents a uniform phase shift,

$$\boldsymbol{\delta} = c_1 \mathbf{v}_1 = c_1 (1, 1, \ldots, 1)^{\mathsf{T}} \tag{72}$$

where $c_1 \in \mathbb{R}$, $|c_1| \ll 1$, and $\mathbf{v}_1$ is the eigenvector of A corresponding to the eigenvalue $\lambda_1 = 1$ (46). Such a perturbation satisfies

$$\boldsymbol{\delta}(T) = A\boldsymbol{\delta} = \boldsymbol{\delta} \tag{73}$$

for all matrices $A = A(\mathrm{rank}(\boldsymbol{\delta}))$ independent of the rank order $\mathrm{rank}(\boldsymbol{\delta})$ and thus

$$\|\boldsymbol{\delta}(T)\| = \|\boldsymbol{\delta}\| \; . \tag{74}$$

Now consider a $\boldsymbol{\delta}$ that does not represent the synchronous state,

$$\boldsymbol{\delta} \neq c_1 \mathbf{v}_1 \tag{75}$$

for all $c_1 \in \mathbb{R}$. Then one might guess that

$$\|\boldsymbol{\delta}(T)\| < \|\boldsymbol{\delta}\| \; . \tag{76}$$

We assume that (i) $\boldsymbol{\delta}$ is not the synchronous state (75) and that (ii) all single-oscillator perturbations are non-negative, $\delta_i \geq 0$. The latter assumption is made without loss of generality, because otherwise a vector proportional to $\mathbf{v}_1$ can be added such that $\delta_i \geq 0$ is satisfied. The assumption (ii) implies that the components of the perturbation stay non-negative for all times, because $\delta_i(T) = \sum_{j=1}^N A_{ij} \delta_j \geq 0$ for all i such that $\delta_i(lT) \geq 0$ for all i and all $l \in \mathbb{N}$.

For convenience, we define the largest component of the perturbation

$$\delta_M := \max_i \delta_i \tag{77}$$

and the second largest component

$$\delta_m := \max\{\delta_i \,|\, \delta_i < \delta_M\} \tag{78}$$

such that $\delta_m < \delta_M$. We also define the index set of maximal components

$$\mathbb{M} := \{j \in \{1, \ldots, N\} \,|\, \delta_j = \delta_M\} \tag{79}$$

which is always non-empty. We write $j \notin \mathbb{M}$ if $j \in \{1, \ldots, N\} \setminus \mathbb{M}$. With these definitions we find

$$\delta_i(T) = \sum_{j=1}^N A_{ij} \delta_j \tag{80}$$

$$= \sum_{j \in \mathbb{M}} A_{ij} \delta_j + \sum_{j \notin \mathbb{M}} A_{ij} \delta_j \tag{81}$$

$$\leq \sum_{j \in \mathbb{M}} A_{ij} \delta_M + \sum_{j \notin \mathbb{M}} A_{ij} \delta_m \tag{82}$$

$$+ \sum_{j \notin \mathbb{M}} A_{ij} \delta_M - \sum_{j \notin \mathbb{M}} A_{ij} \delta_M \tag{83}$$

$$= \delta_M \sum_{j=1}^N A_{ij} - (\delta_M - \delta_m) \sum_{j \notin \mathbb{M}} A_{ij} \tag{84}$$

$$= \delta_M - (\delta_M - \delta_m) \sum_{j \notin \mathbb{M}} A_{ij} \, . \tag{85}$$

Hence if $\sum_{j \notin \mathbb{M}} A_{ij} > 0$ the norm of the perturbation vector *decreases* in one period,

$$\|\boldsymbol{\delta}(T)\| = \max_i \delta_i(T) < \delta_M = \max_i \delta_i = \|\boldsymbol{\delta}\| \, . \tag{86}$$

There are, however, also perturbations that imply $A_{ij} = 0$ for (at least) one specific i and all $j \notin \mathbb{M}$ such that $\sum_{j \notin \mathbb{M}} A_{ij} = 0$. This is the case if and only if there is an oscillator i that receives input only from oscillators j with maximal components, $\delta_j = \delta_M$, and itself has maximal component, $\delta_i = \delta_M$. So suppose that

$$\exists i \in \{1, \ldots, N\} \; \forall j \in \mathrm{Pre}(i) \cup \{i\} \,:\, \delta_j = \delta_M \, , \tag{87}$$

i.e. $\mathrm{Pre}(i) \cup \{i\} \subset \mathbb{M}$. Then $\delta_i(T) = \delta_M$ for this oscillator i and hence

$$\max_i \delta_i(T) = \delta_M \tag{88}$$

such that the norm of the perturbation vector does *not decrease* within one period.

Nevertheless, if the network is strongly connected, the norm of the perturbation vector is reduced in at most $N-1$ periods: We know that if and only if there is no oscillator i satisfying (87), the norm will be reduced (86) because $\sum_{j \notin \mathbb{M}} A_{ij} > 0$ for all i by (85). So to have $\max_i \delta_i(T) = \delta_M$ one needs one oscillator i that satisfies (87), i.e. i and $\mathrm{Pre}(i)$ have to have maximal components. If the vector norm stays maximal another period,

$$\max_i \delta_i(2T) = \delta_M \, , \tag{89}$$

not only all $j \in \{i\} \cup \mathrm{Pre}(i)$ but also all $j \in \mathrm{Pre}(\mathrm{Pre}(i))$ have to have maximal components, $\delta_j = \delta_M$. Iterating this l times, leads to the condition

$$\max_i \delta_i(lT) = \delta_M \; \Leftrightarrow$$

$$\exists i \; \forall j \in \{i\} \cup \mathrm{Pre}(i) \cup \mathrm{Pre}^{(2)}(i) \cup \ldots \cup \mathrm{Pre}^{(l)}(i) \,:\, \delta_j = \delta_M \tag{90}$$

where

$$\text{Pre}^{(l)}(i) := \underbrace{\text{Pre} \circ \text{Pre} \circ \ldots \circ \text{Pre}}_{l \text{ times}}(i) \tag{91}$$

is the set of oscillators, that is connected to oscillator i via a sequence of exactly l directed connections.

Since for a strongly connected network the union of all presynaptic oscillators and their respective presynaptic oscillators is the set of all oscillators

$$\{i\} \cup \text{Pre}(i) \cup \text{Pre}^{(2)}(i) \cup \ldots \cup \text{Pre}^{(l)}(i) = \{1, \ldots, N\} \tag{92}$$

for $l \geq N - 1$, this leads to the conclusion that

$$\max_i \delta_i((N-1)T) = \delta_M \Rightarrow \forall j : \delta_j = \delta_M \tag{93}$$

such that

$$\boldsymbol{\delta} = \delta_M \mathbf{v}_1 \tag{94}$$

contrary to the assumption (75). Note that for a given network connectivity, the condition (92) is satisfied for any $l \geq l_c$ where l_c is the diameter of the underlying network, the longest directed connection path between any two oscillators in the network. The diameter is maximal, $l_c = N - 1$, assumed for a ring of N oscillators.

Hence, after at most l_c periods, the norm of the perturbation vector decreases,

$$\|\boldsymbol{\delta}(lT)\| < \|\boldsymbol{\delta}\| \tag{95}$$

for $l \geq l_c$. Since $\|\boldsymbol{\delta}(ml_cT)\|$ is strictly monotonically decreasing with $m \in \mathbb{N}$ and bounded below by zero, the limit

$$\boldsymbol{\delta}^\infty := \lim_{m \to \infty} \boldsymbol{\delta}(ml_cT) \tag{96}$$

exists. If $\boldsymbol{\delta}^\infty \neq c_1 \mathbf{v}_1$ the vector norm would be reduced as implied by the above considerations. Thus we find that

$$\boldsymbol{\delta}^\infty = c_1 \mathbf{v}_1 \tag{97}$$

because the uniform components $c_1 \mathbf{v}_1$ of the original perturbation $\boldsymbol{\delta}$ does not change under the dynamics (see Eq. (73)). This completes the demonstration that the synchronous state is asymptotically stable for any strongly connected network of inhibitorily coupled oscillatory units.

VIII.   SUMMARY AND DISCUSSION

We analyzed the stability of synchronous states in arbitrarily connected networks of pulse-coupled oscillators. For generally structured networks, the intricate problem of multiple stability operators arises. We analyzed this multi-operator problem exactly. For both inhibitory and excitatory couplings, we determined analytical bounds on the eigenvalues of all operators. Given the multi-operator property, stability cannot be deduced by considering the eigenvalues only. We therefore completed the stability analysis on two levels For networks with inhibitory couplings ($\varepsilon_{ij} \leq 0$) we found plain (Lyapunov) stability of the synchronous state; under mild constraints (strong connectivity of the network), graph theoretical arguments show that it is also asymptotically stable, independent of the parameters and the details of the connectivity structure.

Let us point out that the stability results obtained here are valid for arbitrarily large finite networks of general connectivity. In contrast to ordinary stability problems, the eigenvalues of the first order operators do not directly determine the stability here, because different linear operators may act subsequently on a given perturbation vector. Thus the eigenvalues and eigenvectors of an individual matrix alone do not define the local dynamics of the system. For network dynamical systems of pulse-coupled units that exhibit more complex cluster states, with two or more groups of synchronized units, an analogous multi-operator problem arises [23, 24, 35]. Methods to bound their spectra and the graph theoretical approach presented above to prove asymptotic stability are applicable to these cluster states in a similar way, provided the stability problem is originally formulated in an event-based manner. Further studies (e.g., [29]) show that the stable synchrony in complex networks is not restricted to the class of models considered here. Together with other works, e.g. [31, 32, 34], this also indicates robustness of the synchronous state against structural perturbations, i.e. conditions necessary to ensure that the local dynamics stays qualitatively similar if the time evolution of the model is weakly modified.

It has been hypothesized (see e.g. [49, 50]) that the experimentally observed precisely timed firing patterns in otherwise irregular neural activity might be generated dynamically by the cerebral cortex. As a by-product, our results clearly demonstrate that states in which units fire in a temporally highly regular fashion and states with irregular asynchronous activity may be coexisting attractors of the same recurrent network, cf. [38]. This already applies to random networks. More specifically structured networks may possess a large variety of dynamical states in which firing times are precisely coordinated. A promising direction for future research is thus to adopt the methods developed here for investigating the stability of such states. In particular, methods adapted from the ones developed here may reveal dynamical features of networks in which the coupling strengths are not only structured but highly heterogeneous and precise temporal firing patterns occur in place of a simple synchronous state [29, 34, 36]. More generally, our methods may help to understand properties of stability and robustness in various network dynamical systems with pulsed interactions. They may thus be relevant not only for networks of nerve cells in the brain coupled via chemical synapses but also for cells in heart tissue coupled electrically and even for populations of fireflies and chirping crickets that interact by sending and receiving light pulses and sound signals, respectively.

IX.   APPENDIX: EXACT DERIVATION OF THE EXPANSION (34)

We prove a generalization of the first order expansion (34) used above,

$$\beta_{i,m} \doteq \alpha_{i,m} + \sum_{n=1}^{m} p_{i,n-1,m}\, D_{i,n} \quad \text{for} \quad m \in \{1,\ldots,k_i\}, \tag{98}$$

by induction over m for arbitrary fixed $i \in \{1,\ldots,N\}$. As in the main text, here the statement $x \doteq y$ means that $x = y + \sum_{i,n} \mathcal{O}(D_{i,n}^2)$ as all $D_{i,n} \to 0$. The quantities $\beta_{i,m}$ were defined in Table I . The quantities (98) appear in the derivation of the map (32) for $m = k_i$. As an extension of the notation in section IV, we denote here

$$\alpha_{i,m} = U^{-1}\left(U(\tau) + \sum_{n=1}^{m} \varepsilon_{ij_n} \right) \quad \text{for} \quad m \in \{0,\ldots,k_i\}, \tag{99}$$

$$D_{i,n} = \Delta_{i,n-1} - \Delta_{i,n} \quad \text{for} \quad n \in \{1,\ldots,k_i\}, \tag{100}$$

and

$$p_{i,n,m} = \frac{U'(\alpha_{i,n})}{U'(\alpha_{i,m})} \quad \text{for} \quad 0 \le n \le m \le k_i. \tag{101}$$

Here the prime denotes the derivative of the potential function U with respect to its argument. The latter definition implies the identity

$$p_{i,n,l}\, p_{i,l,m} = p_{i,n,m}. \tag{102}$$

For the case $m = 1$, the induction basis, expression (98) holds because

$$\begin{align}
\beta_{i,1} &= U^{-1}(U(\tau + D_{i,1}) + \varepsilon_{ij_1}) \tag{103}\\
&\doteq U^{-1}(U(\tau) + \varepsilon_{ij_1}) \tag{104}\\
&\quad + \left[\frac{\partial}{\partial D} U^{-1}(U(\tau + D) + \varepsilon_{ij_1}) \right]_{D=0} D_{i,1}\\
&= \alpha_{i,1} + \frac{U'(\tau)}{U'(U^{-1}(U(\tau) + \varepsilon_{ij_1}))} D_{i,1} \tag{105}\\
&= \alpha_{i,1} + \frac{U'(\alpha_{i,0})}{U'(\alpha_{i,1})} D_{i,1} \tag{106}\\
&= \alpha_{i,1} + p_{i,0,1}\, D_{i,1} \tag{107}
\end{align}$$

where the third last equality holds because the derivatives of inverse functions are given by $\partial/\partial x\, U^{-1}(x) = 1/U'(U^{-1}(x))$. The induction step, $m \mapsto m+1$, is proven by

$$\beta_{i,m+1} = U^{-1}(U(\beta_{i,m} + D_{i,m+1}) + \varepsilon_{ij_{m+1}}) \tag{108}$$

$$\doteq U^{-1}\left(U\left(\alpha_{i,m} + \sum_{n=1}^{m} p_{i,n-1,m}D_{i,n} + D_{i,m+1}\right) + \varepsilon_{ij_{m+1}}\right) \tag{109}$$

$$\doteq U^{-1}\left(U\left(\alpha_{i,m}\right) + \varepsilon_{ij_{m+1}}\right) \tag{110}$$

$$+ \left[\frac{\partial}{\partial D}U^{-1}(U(\alpha_{i,m} + D) + \varepsilon_{ij_{m+1}})\right]_{D=0}\left(\sum_{n=1}^{m} p_{i,n-1,m}\, D_{i,n} + D_{i,m+1}\right)$$

$$= U^{-1}\left(U\left(\alpha_{i,m}\right) + \varepsilon_{ij_{m+1}}\right) + \frac{U'(\alpha_{i,m})}{U'(\alpha_{i,m+1})}\left(\sum_{n=1}^{m} p_{i,n-1,m}\, D_{i,n} + D_{i,m+1}\right) \tag{111}$$

$$= \alpha_{i,m+1} + p_{i,m,m+1}\left(\sum_{n=1}^{m} p_{i,n-1,m}\, D_{i,n} + D_{i,m+1}\right) \tag{112}$$

$$= \alpha_{i,m+1} + \sum_{n=1}^{m+1} p_{i,n-1,m+1}\, D_{i,n} \tag{113}$$

where we used $U(\alpha_{i,m}) + \varepsilon_{ij_{m+1}} = U(\alpha_{i,m+1})$ in the second last step and the identity (102) in the last step. This completes the proof of the first order expansion (98).

Note that because of the normalization $\sum_{n=1}^{k_i} \varepsilon_{ij_n} = \sum_{j=1}^{N} \varepsilon_{ij} = \varepsilon$ for all i, the quantity $\alpha_{i,k_i} = U^{-1}(U(\tau) + \varepsilon) = \alpha$ is independent of i. In addition, $p_{i,n,k_i} = p_{i,n}$ for all i and all n. Hence, theorem (98) in the case $m = k_i$ yields expression (34).

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